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New Habitat Report for *Maldivia triunguiculata* (Borradaile) (Brachyura, Xanthidae), a Facultative Symbiont of *Porites lobata* Dana in Hawaii[1]

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ABSTRACT: *Maldivia triunguiculata* (Borradaile), a xanthid crab, lives within chambers in the skeletons of live *Porites lobata* corals. The chamber openings are readily recognizable on the live surfaces of *P. lobata* heads, and chambers penetrate into coral skeletons up to 5.5 cm. Crabs inhabited an average of 85 percent of the chambers investigated. Occupied chambers contained males or females, but never more than one crab per chamber. Areal density of *M. triunguiculata* on *P. lobata* increased with increasing coverage of the reef by the live coral, indicating a strong association between the two species. Although *M. triunguiculata* may occur on dead coral reef, this study indicates that it is more frequently found in live *P. lobata*.

LIVING REEF CORAL provides habitat for a variety of decapod crustaceans which live in one of two types of symbiotic association with their coral hosts: (1) motile, ectocommensal crabs and shrimp living upon branching live coral skeletons that shield them from predators and probably provide them with a food or food supplement in the form of coral mucus (Abele 1976, Abele and Patton 1976, Barry 1965, Castro 1978, Coles 1980, Garth 1964, 1974*a*, *b*, Patton 1966, 1974, Preston 1971, 1973); and (2) crabs that live within a coral skeleton, either in chambers that penetrate the coral well below the surface or in galls that form on the coral's surface when a crab settles in the juncture of a branch (Edmondson 1933, Fize and Serene 1957, Garth and Hopkins 1968, Henderson 1906, Hiro 1937, McCain and Coles 1979, Patton 1967, Potts 1915, Serene 1962, 1966, Shaw and Hopkins 1977, Utinomi 1944). With few exceptions (Patton 1967, Patton and Robertson 1980), decapods living within coral skeletons are members of the family Hapalocarcinidae. Hapalocarcinids are highly modified structurally for their chamber existence, with reproductively mature females usually unable to leave their chambers.

During diving surveys in the vicinity of Kahe Point, Oahu, Hawaii, I noted burrow openings on the surface of *Porites lobata* that were very similar to burrow openings of the hapalocarcinid crab *Pseudocryptochirus kahe* (McCain and Coles 1979) in *Pocillopora meandrina* Dana. Investigation of these burrows in *Porites lobata* revealed that they were occupied not by a hapalocarcinid as was anticipated, but by the xanthid crab *Maldivia triunguiculata* (Borradaile). This species of crab has previously been reported by a number of authors (Borradaile 1902, Edmondson 1962, Garth 1969, 1974*b*, Guinot 1964, Rathbun 1906, 1911, Sakai 1976), but the characteristics of its association with a live coral host have never been described.

My findings indicate that this crab is facultatively symbiotic with *Porites lobata* in Hawaii and that the occurrence of a burrow opening on a *P. lobata* head usually indicates the presence of a crab within the burrow.

METHODS

Nine stations in the Kahe Point, Oahu, nearshore area were investigated for their populations of *Maldivia triunguiculata*. At

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each station, areas of live *Porites lobata* coral were estimated using a 1-m frame subdivided into 100 square subsections, and the number of *M. triunguiculata* chamber openings on *P. lobata* were counted. This produced estimates of chamber density per area of live *P. lobata*. Percent coverage by *P. lobata* was known for each station from previous surveys for transects totaling 20 m^2 at each station. Multiplying chamber density times area of *P. lobata* habitat provided estimates of total abundance of *M. triunguiculata* burrows throughout the study area.

Rates of occupancy of burrows were checked in the field by splitting coral heads with a diver's tool and hammer. Where possible, occupants of burrows were captured, returned to the laboratory, and examined as to size, sex, and sexual maturity. In addition to these census data, 20 coral heads containing burrows were removed to the laboratory for more intensive analyses. Burrow opening and depth were measured on these corals and compared with carapace size and sex of the crab occupants.

RESULTS AND DISCUSSION

Abundance of *Maldivia triunguiculata* on the reef was strongly associated with areal coverage of *Porites lobata*. Numbers of chambers per area of live *P. lobata* (chamber density) increased with increasing percent cover of the bottom by *P. lobata*. A linear regression between chamber density and *P. lobata* coverage was highly significant ($F < 0.03$, $n = 7$), with 65 percent of the variance in chamber density explained by *P. lobata* coverage.

Occupancy of the chambers by *Maldivia triunguiculata* was high, averaging 85 percent (range = 66 – 100 percent) at the nine stations surveyed. Approximately two-thirds of the occupied chambers contained females, and about one-third of the females carried eggs. No clear relationship was determined between crab size and egg-bearing. For example, three crabs with carapace widths of 2.4–3.1 mm were found with eggs at one station, while at another station sampled 1 month later none of five females with widths 3.5–4.8 mm carried eggs.

Although *Maldivia triunguiculata* was much more abundant in live *Porites lobata*, chambers occupied by crabs were found on dead reef material at two stations in this survey. In one case, a chamber and crab were found in a head of *Pocillopora meandrina* that I estimated to have been dead at least 2 yr. This indicates that the association between *M. triunguiculata* and *P. lobata* is facultative and may be particularly pronounced in Hawaii, where *P. lobata* occupies a major portion of the available space on nearshore, leeward coral reefs.

Maldivia triunguiculata chambers can be recognized in the field by characteristic ellipsoid openings on the live surfaces of *Porites lobata* (Figure 1). The ellipsoid shape of the openings distinguishes them from circular sabellid or vermetid worm tube openings that may also be found on *P. lobata*. *Maldivia triunguiculata* chamber openings in this study ranged from 3.3 to 8.8 mm in largest dimension.

Although the shape of the *Maldivia triunguiculata* chamber opening is usually quite regular, the interior of the burrow chamber is highly variable in both dimension and shape (Figure 2). Generally, the outer 1-cm section of a chamber is relatively straight, but below this the section may be enlarged and curved. Depth of the chambers measured in this study ranged from 4.2 to 55.0 mm. In the zone of active coral growth along a chamber's periphery, the chamber is often lined with a growth of calcareous algae. Below this zone the chamber extends to a terminus that usually conforms closely to the occupant crab's external configuration.

During field surveys, crabs were sometimes observed facing out of their chambers, just below the chamber openings. The shape and dimensions of a *Maldivia triunguiculata* chamber opening generally conforms closely to the cross-sectional area of the crab the chamber contains. Highly significant linear regression coefficients were found between crab carapace width and chamber opening long dimension ($F < 0.001$, $n = 21$) and between carapace dorsal-ventral thickness and

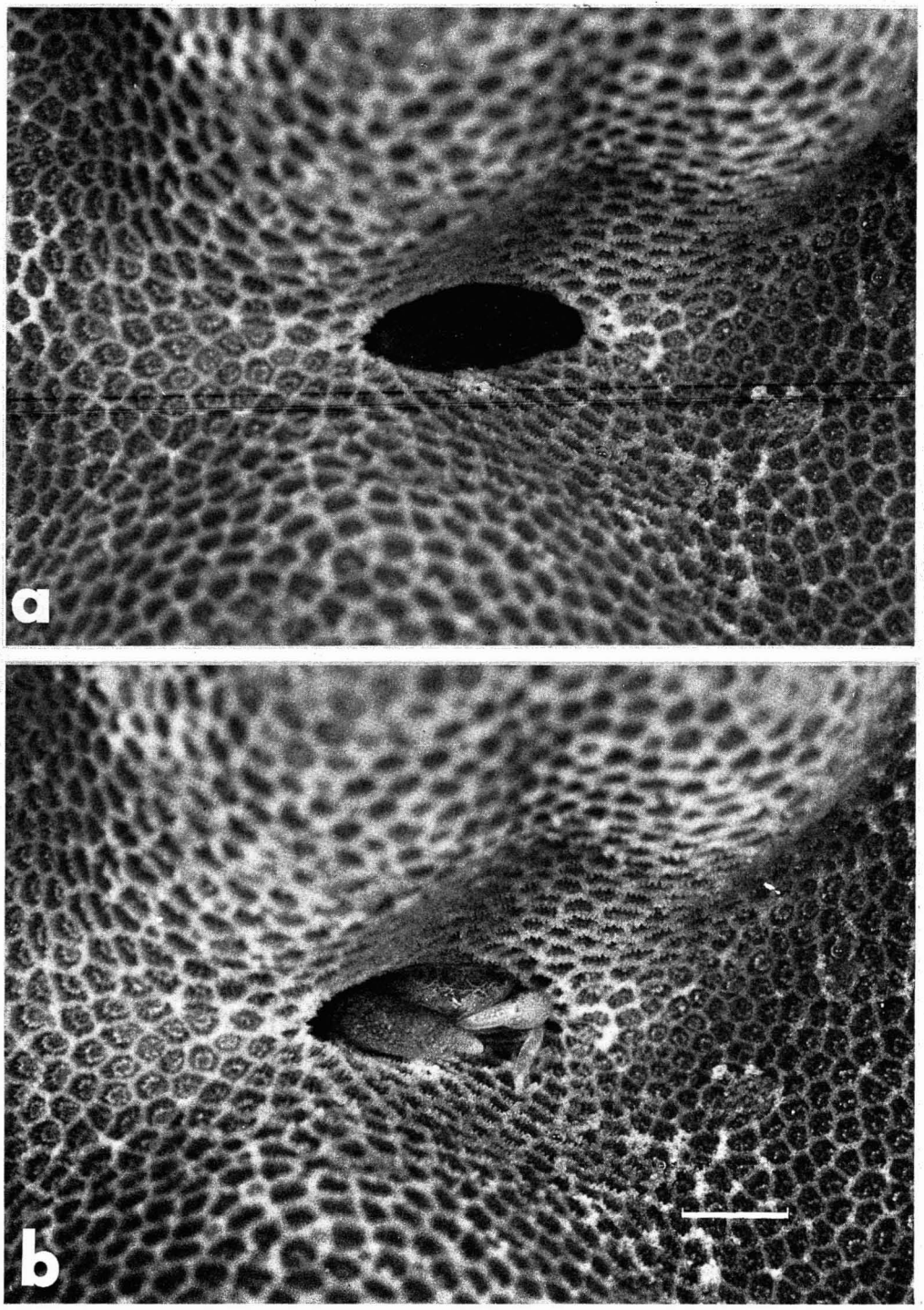

FIGURE 1. Entrance of *Maldivia triunguiculata* chamber on surface of *Porites lobata*. *a*, usual appearance; *b*, resident crab at chamber entrance. (Scale equals 5 mm.)

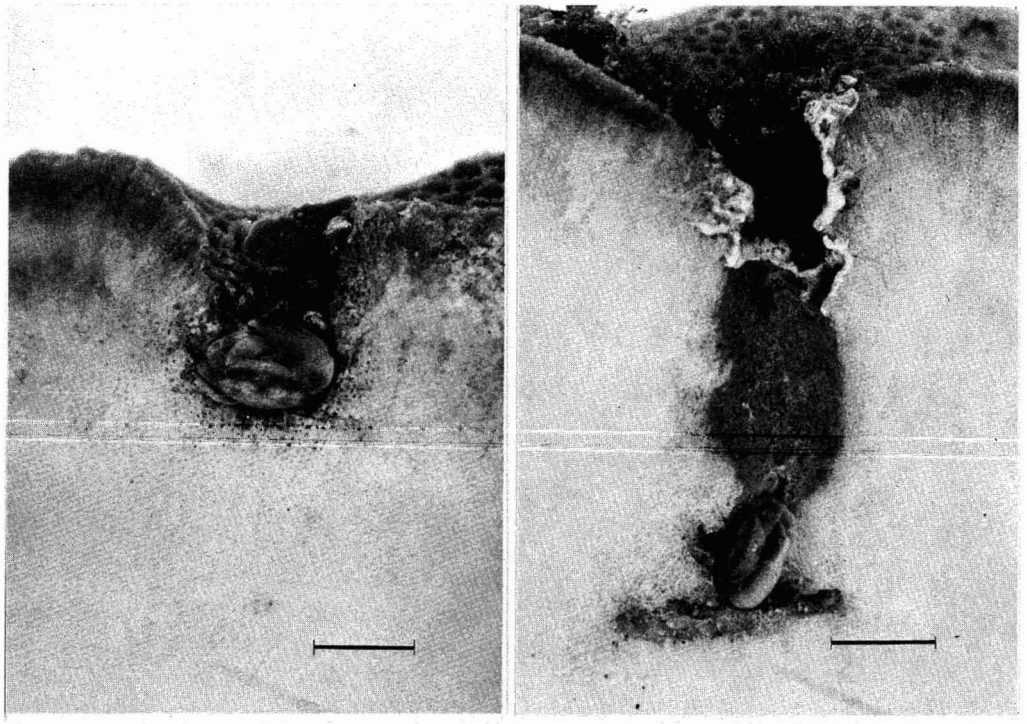

FIGURE 2. Longitudinal sections of two *Maldivia triunguiculata* chambers containing crabs. (Scales equal 5 mm.)

chamber opening short dimension ($F < 0.001$, $n = 21$). The close conformation between crab dimensions and chamber openings indicates that *M. triunguiculata* actively forms its chamber rather than merely occupying cavities vacated by other organisms.

The mechanism by which *Maldivia triunguiculata* forms chambers may be similar to that previously described for *Cryptochirus* and similar hapalocarcinid crabs (Hiro 1937, McCain and Coles 1979, Potts 1915, Utinomi 1944). In these species a small crab settles on a coral surface and the chamber is produced by growth of coral skeleton around the crab. It is uncertain whether these crabs have any capability to enlarge or modify the chamber other than by movement of water to increase coral skeleton growth rate. However, in *M. triunguiculata*, cross-sectional chamber dimensions so closely correspond to crab dimensions, that it is likely that a crab must enlarge its chamber to accommodate its own growth, possibly by secretion of a calcium carbonate dissolving enzyme. Also, the occasional occurrence of occupied chambers in non-*Porites* coral reef material indicates an active mechanism for chamber formation independent of coral growth.

Chambers up to 5.5 cm deep were found in this study. *Porites lobata* vertical growth rates in Hawaii have been estimated to average from 7.1 mm/yr (Edmondson 1929) to 10.9 mm/yr (Maragos 1972). Thus, in order for the occupant of the deepest chamber to have formed the chamber, given that it did not deepen the chamber after settlement, the crab would have to be 5–7 yr old. More likely explanations of chamber depth are that the crab is capable of deepening the chamber or that occupants may die or leave the chamber from time to time, providing a habitat for another crab which then occupies and maintains the chamber.

The latter possibility is suggested by the fact that about 15 percent of the chambers were found empty in this study. Potts (1915) and Hiro (1937) have proposed similar sequential occupation of chambers by *Cryptochirus* crabs, as has Patton (1967) for the xanthid *Domecia acanthophora*.

Of all published reports on *Maldivia triunguiculata* only Borradaile (1902), who originally described the species as *Pseudozius triunguiculatus*, has suggested a symbiotic relationship for it with a host coral. He noted structural modifications in walking appendages and the body that "give the impression that the crabs are indeed symbiotic with the coral, living always on its surface, but take refuge in the *Cryptochirus* holes at times only." Borradaile's holotype specimen was taken from a head of the faviid coral, *Leptoria tenuis*.

The present study indicates a much closer relationship between *Maldivia triunguiculata* and a host coral than was described by Borradaile (1902). Chambers are formed by *M. triunguiculata* itself, not by *Cryptochirus*, a genus of hapalocarcinid. *Maldivia triunguiculata* was never observed outside a chamber, although it was sometimes observed just below the chamber opening. No hapalocarcinids of any species were found in more than 60 chambers examined, and no hapalocarcinids have been previously reported to inhabit any species of *Porites* (Fize and Serene 1957).

The only other published report of a chamber-forming xanthid crab in live coral is of *Domecia acanthophora* in Caribbean *Acropora* (Castro 1976, Patton 1967, 1976). In contrast to the often deep chambers of *Maldivia triunguiculata*, chambers formed by *D. acanthophora* are pitlike and not much deeper than the crab's body. The *D. acanthophora* pits result from growth of the rapidly growing *Acropora* around and over crabs in preferred resting places on live coral.

Chamber habitation in live coral has recently been reported for the first time for a pagurid crab, *Paguritta harmsi*, in the massive coral *Astreopora myriopthalma* (Patton and Robertson 1980). The chamber dimensions and structure described for *P. harmsi* are quite similar to the chambers of *Maldivia triunguiculata* and chamber-forming hapalocarcinid crabs. Chamber-forming behavior by decapods is therefore more universal than formerly realized, and is probably an adaptation of previously nonsymbiotic decapods to habitat opportunities provided by the large surface areas of massive reef corals. With the exception of *Pseudocryptochirus kahe*, which inhabits branching *Pocillopora* (McCain and Coles 1979), all the chamber-dwelling crabs occupy corals that are massive and have relatively smooth, lobate surfaces. Crabs occupying their surfaces would have little or no protection from predators without the formation of a chamber. The mechanisms by which a juvenile crab selects a chamber site, how it is able to survive the initial stages of chamber formation without being eaten, and whether the crab secretes enzymes that facilitate chamber formation would be interesting topics for further research.

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